CYTOLOGICAL, MORPHOLOGICAL, ECOLOGICAL AND PHENOLOGICAL SUPPORT FOR SPECIFIC STATUS OF *CRATAEGUS SUKSDORFII* (ROSACEAE)

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ABSTRACT

Field and herbarium studies have revealed the presence of 20-stamen black-fruited hawthorns (*Crataegus*) from 29 sites in the northern Rocky Mountains. This entity has often been treated as a variety of the 10-stamen species, *C. douglasii,* and was formerly believed to be essentially restricted to west of the Cascade/Sierra Range. We present evidence that the 20-stamen form is diploid whereas *C. douglasii* is tetraploid, and that the two differ substantially in morphology, ecology and phenology. These lines of evidence strongly support Kruschke's treatment of the 20-stamen entity as a distinct species, *C. suksdorfii.*

The black-fruited hawthorns, Sect. *Douglasii* Loud., constitute the most widespread and abundant members of *Crataegus* L. in western North America. The group consists of three entities that have been treated as distinct species (Kruschke 1965), or as varieties of one species, *Crataegus douglasii* Lindl. (e.g., Hitchcock et al. 1961; Scoggan 1978). *Crataegus suksdorfii* (Sarg.) Kruschke (*C. douglasii* var. *suksdorfii* Sarg.) is distinctive in having 20 stamens, and was previously thought to be distributed: "entirely west of the Cascades except inland somewhat in the Fraser R. Valley and Columbia R. Gorge" (Hitchcock et al. 1961); and confined to the "Coastal Douglas-Fir" zone in British Columbia (Taylor and MacBryde 1977). The second form, *C. douglasii* (var. *douglasii*), has 10 stamens and is widespread in the northern Rocky Mountain region, occurring occasionally west of the Cascades in the Puget Sound and the Columbia River Gorge, and also disjunct in northern Michigan and southwestern Ontario (Hitchcock et al. 1961). The third form, *C. rivularis* (var. *rivularis*), has 10 stamens, is distributed in the central Rocky Mountains, and differs from *C. douglasii* in its leaf shape and branching pattern. *Crataegus rivularis* is poorly understood and will not be considered further in this paper.

Differences in stamen number, especially 10 vs. 20 stamens, are found in many species groups in *Crataegus*. Some early workers (e.g., Eggleston 1908; Palmer 1946) considered this variation relatively trivial and did not use stamen number as an important basis for distinguishing species. Kruschke (1965), however, placed con-

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siderable weight on this trait; he stated "a 10-stamen entity can not be a variety of a 20-stamen entity or conversely so". On this basis, and perhaps other unmentioned characters, he elevated many taxa, including *C. suksdorfii,* to specific status. Phipps and Muniyamma (1980) have noted that taxa differing in stamen number generally have other associated distinguishing features.

The recent discovery of 20-stamen hawthorns sympatric with 10-stamen forms in the northern Rocky Mountains has prompted a reevaluation of the taxonomy of these two entities. Our investigations provide evidence from cytology, morphology, ecology, and phenology that *C. suksdorfii* should indeed be considered a distinct species.

Distribution

Since 1981, when a specimen of 20-stamen *Crataegus* from Idaho first came to our attention (*Wellner 2258*), we have gathered extensive field and herbarium data (ID, IDF, MONTU, MRC, ORE, WS, UW) on the black-fruited hawthorns of the northern Rocky Mountain region. Figure 1 illustrates the formerly-known western distribution of *C. suksdorfii,* and the locations of 29 newly-confirmed northern Rocky Mountain populations (representative specimens are given in Table 1). The disjunct range extends from about latitude 49° to 53°N, a distance of about 1000 km. Inland Rocky Mountain and coastal populations are disjunct 200–400 km from one another throughout most of their range, but the gap is somewhat bridged by populations in the Fraser R. drainage in interior British Columbia, and three isolated collections from east of the Cascade crest in central Washington and Oregon (Fig. 1). The two Washington sites are from the east slope of Cascades, east of the formerly-described range, but following a pattern seen in many other "west side" species such as *Cornus nuttallii* and *Acer circinatum* (Hitchcock et al. 1961). The third outlier, in central Oregon, appears to be a continuation of the Columbia River Gorge eastward extension of range. The type locality of *C. suksdorfii,* indicated by an open circle in Figure 1, is at the east end of the Columbia River Gorge in Klickitat Co., Washington. Figure 1 also shows the principal range of *C. douglasii,* which is partially sympatric with the disjunct inland *C. suksdorfii* element reported here. Herbarium data also confirm that there is localized sympatry in the Puget Sound/Vancouver Island region and the Columbia River Gorge. We have not examined the extent of sympatry or the ecological relationships between the species at these western points of contact.

Evidence for Specific Status of *Crataegus suksdorfii*

Species concepts in *Crataegus* have been notoriously variable. For example, estimates by various workers for the number of *Crataegus*

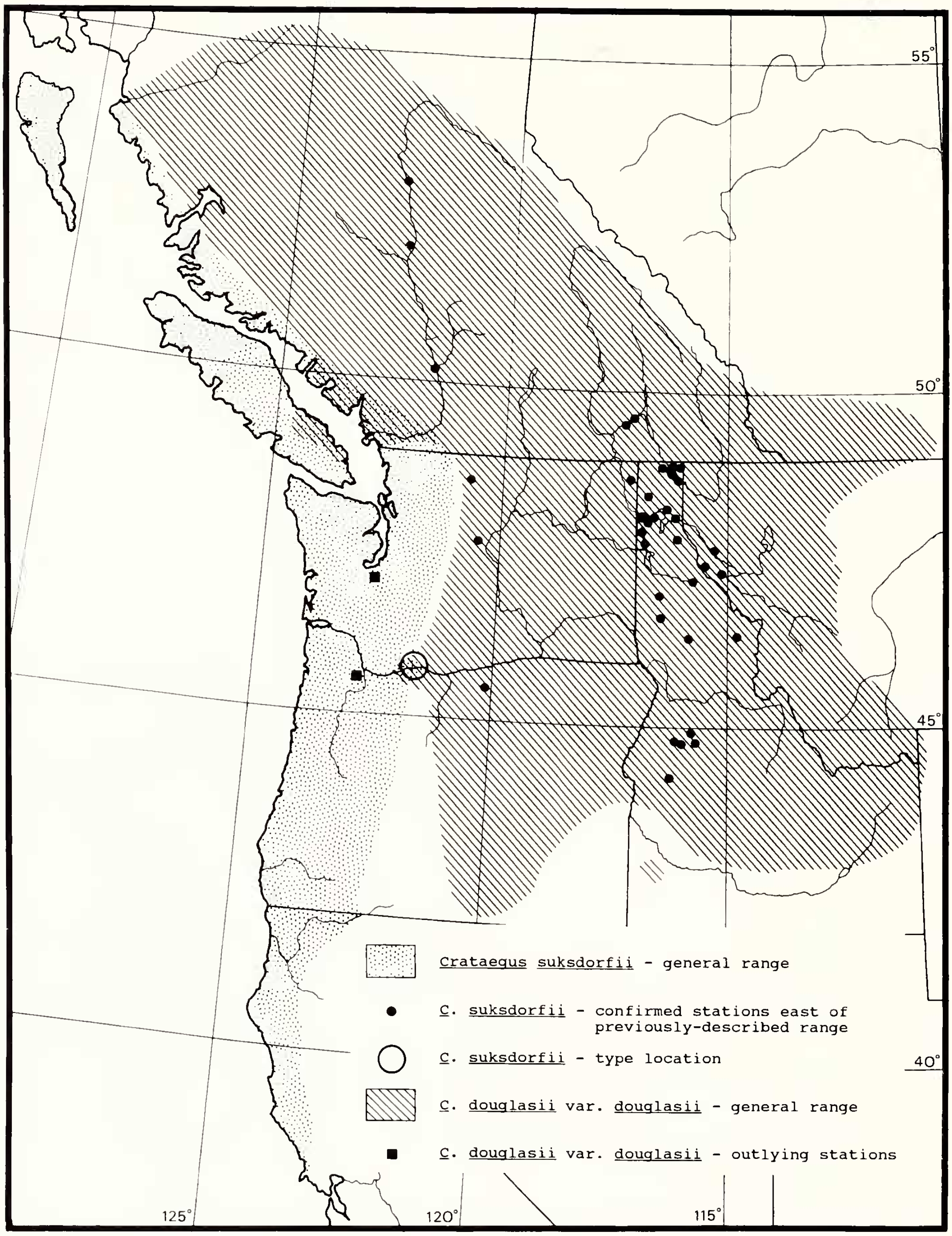

Fig. 1. Ranges of *Crataegus suksdorfii* and *C. douglasii* (var. *douglasii*). Generalized ranges based on Little (1976), herbarium data and floras cited in text.

species in Ontario range from 8 to 91 (Phipps and Muniyamma 1980). Until recent years species concepts were based largely on the principal data at hand: morphology seen on herbarium sheets. In modern biosystematic studies decisions on what constitutes a species are generally based on assessments of the reproductive biology and the overall genetic divergence of the populations under consider-

TABLE 1. REPRESENTATIVE SPECIMENS OF *CRATAEGUS SUKSDORFII* FROM THE INTERIOR/ROCKY MOUNTAIN REGION.

Canada, British Columbia, Willow Point, Kootenay Lake, 49°33'N, 117°15'W, *Eastham 9022* (UBC); Quesnel Dam, 52°58'N, 122°30'W, *Newcombe 377* (UBC). United States, Idaho: Boundary Co., Smith Lake, *Johnson and Brunsfeld 1954* (ID, IDF); Hideaway Island, Kootenai R., *Wellner 2258* (ID); Bonner Co., Priest River Exp. Forest, *Daubenmire 44264* (WS); Kootenai Co., E fork of Hayden Ck, vic. Hayden Lake, *Johnson 86134* (ID, IDF); Shoshone Co., Coeur d'Alene R. vic. Spion Kop Ck., *F. D. Johnson and C. L. Johnson 1574* (ID, IDF); Benewah Co., St. Maries R. vic. Soldier Ck., *Brunsfeld and Johnson 2802* (ID, IDF); Idaho Co., Lochsa R. at Wendover Ck., *Johnson and Brunsfeld 2800* (ID, IDF); Valley Co., Middle Fork Payette R. vic. Trail Ck. Campground, *Kramer N192* (IDF). Montana: Missoula Co., Miller Ck., *Hitchcock 1762* (MONTU); Mineral Co., 0.5 mi E of Lookout Pass, *Johnson and Smith s.n.* (IDF)., Washington: Pend Oreille Co., Sullivan Lake, *Johnson 8931* (ID, IDF); 6 mi N of Newport, *Jones 5645* (WTU).

ation. If a group of populations is reproductively isolated and possesses significant genetic distinctions, as manifested by morphology, ecology, phenology, molecular measures, etc., the criteria of both the biological species concept and the taxonomic species concept are satisfied (Grant 1981). We present four lines of evidence that together strongly support the treatment of *C. suksdorfii* as a biological and taxonomic species.

1) *Cytology.* Polyploidy is a common phenomenon in plants, and it generally results in speciation because ploidal differences effectively end most gene exchange (Grant 1981). The 10- and 20-stamen hawthorns considered here exist at different ploidal levels, and thus likely have a high degree of reproductive isolation. *Crataegus suksdorfii* is diploid ($2n=34$) in its distribution west of the Cascade Range (Calder et al. 1968: Queen Charlotte Islands, B.C., $2n=34$). *Crataegus douglasii* has been reported to be tetraploid ($2n=68$). The tetraploid count, however, was from a plant of unknown origin cultivated in Leningrad, USSR (Gladkova 1968). The chromosome number of *Crataegus douglasii* is listed as $2n=51$ in the Flora of Alberta (Moss 1983), but no additional information is given.

We sought to confirm differences in ploidy level of 10- and 20-stamen populations from the sympatric Rocky Mountain region. Flower buds were fixed using standard techniques (Soltis 1980), and mitotic figures were obtained from preparations of tissue from young, meristematic petals (Dickinson and Phipps 1986). No pretreatment of the buds was performed. Counts were obtained from a site where both the 10- and 20-stamen entities occur: USA, Idaho, Adams Co., Goose Ck. near Last Chance Campground, *Cronk 205—Crataegus suksdorfii,* $2n=34$ (ID, IDF); *Cronk 192—Crataegus douglasii,* $2n=68$ (ID, IDF). An additional count of *C. douglasii* was obtained from

TABLE 2. CONSPECTUS OF MORPHOLOGICAL CHARACTERS OF *CRATAEGUS DOUGLASII* (VAR. *DOUGLASII*) AND *C. SUKSDORFII*.

Character	*C. douglasii*	*C. suksdorfii*
Flower width, dried (mm)	14–16	12–13
Stamen number	10	20
Mature fruit, fresh diameter (mm)	9–10	7–8
Pyrene length (mm)	5.0	4.5
Pyrene shape	dorsally rounded, plump, shallowly sculpted laterally	dorsally keeled, narrow, deeply sculpted laterally
Leaf shape on short shoots	obovate, lobed above middle, truncate apex	elliptic to obovate, unlobed, rounded apex
Thorn length on older branches (mm)	13–18	8–12

a population about 280 km to the north: USA, Washington, Whitman Co., vic. Pullman-Moscow Airport, *Brunsfeld 3012,* $2n=68$ (IDF). Photomicrographs and camera-lucida drawings are on file with the authors. We conclude from this evidence that *C. suksdorfii* and *C. douglasii* are diploid and tetraploid, respectively. However, the possible triploid count for *C. douglasii* reported from Alberta may indicate that hybridization, or apomixis and fertilization of unreduced gametes occurs in this species as it does in some other polyploid hawthorns (Dickinson and Phipps 1986; Campbell and Dickinson 1990).

2) *Morphology.* Based on our field and herbarium observations, especially on Rocky Mountain populations, *Crataegus suksdorfii* differs substantially from *C. douglasii* in its floral and vegetative morphology (Table 2, Fig. 2). Because the species differ in flower, fruit, leaf and thorn, they can be distinguished with some certainty throughout the year. Thus they appear to be more clearly differentiated than a number of other recognized species pairs in *Crataegus* (Phipps and Muniyamma 1980).

3) *Ecology.* The discovery of numerous sympatric populations of these two entities allows a comparison of their ecological amplitudes. It has been observed that polyploid species often occupy a wider range of habitats than their diploid relatives (Stebbins 1971; Lewis 1980; Levin 1983). Thus polyploids are often able to tolerate temperature, moisture or soil conditions unsuitable to the diploid. This is clearly the case in this species pair.

In the northern Rockies, *C. suksdorfii* is almost exclusively found in cool, moist stream- and lakeside habitats within forest communities ranging from mid-montane (*Abies grandis, Thuja plicata,* and

Fig. 2. *Crataegus suksdorfii* (left) and *Crataegus douglasii* (right) from same locality: Idaho, Adams Co., Goose Cr. at junction with State Hwy. 55, *F.D. Johnson 88068* and *88069* (IDF), both collected 10 August 1988.

Tsuga heterophylla) to the lower subalpine (*Abies lasiocarpa*) zones. The geographic distribution of *C. suksdorfii* (Fig. 1) conforms to the extent of maritime (coastal) climates in the Rocky Mountains, as manifested by the distribution of *Abies grandis.*

Crataegus douglasii has a substantially broader ecological amplitude in both temperature and moisture regimes. Habitats in the sympatric region range from low-elevation grassland and sagebrush zones, through the montane and lower subalpine forest zones. It inhabits streamside and bottomland sites, but also is common in seasonally drier, mesic, forested and nonforested upland habitats. For example, Cooper et al. (1987) present data for its occurrence beneath near climax upland stands of *Pinus ponderosa, Pseudotsuga menziesii* var. *glauca, Abies grandis,* and *Thuja plicata.* Daubenmire (1970) describes communities dominated by *Crataegus douglasii* in both riparian and upland habitats of the steppe region of Washington.

Crataegus douglasii is so ubiquitous in the Rocky Mountains, it not surprising that it was found in close proximity to many *C.*

suksdorfii populations. At these sites the species tend to be segregated: *C. suksdorfii* at lake or streamside, *C. douglasii* in adjacent meadows and uplands.

4) *Phenology and reproductive biology.* Where we have observed the species occurring together, *C. douglasii* begins flowering one to two weeks before *C. suksdorfii,* though there is some overlap in flowering times. Other workers have also documented differing phenologies for different *Crataegus* species at a site (e.g., Phipps and Muniyamma 1980; Dickinson and Phipps 1986). Fruiting phenology is reversed, with ripe, black fruits present on *C. suksdorfii,* while at the same time and site the fruits of *C. douglasii* are still largely immature. Apparently the larger fruits of tetraploid *C. douglasii* take several weeks longer to develop. Such developmental differences have been observed in other diploid/tetraploid species pairs (Levin 1983).

Despite the large number of populations in the newly-reported range, several lines of evidence suggest a limited reproductive potential for *C. suksdorfii* in this region. Most of the 29 populations reported here contain relatively few individuals and are of restricted geographic extent. This may reflect limited suitable habitat at many sites, but may also be the result of low seed output. We observed a high rate of seed abortion in *C. suksdorfii,* something also noted by Sargent (1907). In many populations we found that frequently at least 3 of the 5 pyrenes per fruit were unfilled. *Crataegus suksdorfii* has been reported to be self-incompatible (Love and Feigan 1978), which combined with small, isolated populations could affect fecundity. We did not observe a notable incidence of seed abortion in *C. douglasii.* Although many of the *C. suksdorfii* populations reported here are in close proximity to larger *C. douglasii* populations, *C. suksdorfii* appears be largely maintaining its identity, probably due to intersterility conferred by ploidal differences and phenological and habitat separation. However, at several locations plants were collected that appear be intermediate or atypical in thorn length and/or leaf characteristics. Additional study of the reproductive biology of these species is needed, particularly to the assess the role of apomixis in *C. douglasii.*

Discussion

The discovery of widespread populations of *C. suksdorfii* in the Rocky Mountains is not only of phytogeographical interest, but also provides insights into the relationship between *C. suksdorfii* and its sister taxon *C. douglasii.* Although it is remarkable that such a widespread and conspicuous species could go undetected until now, the presence of another Pacific coastal species in the northern Rocky Mountain flora is no surprise. Montane vegetation of the western portion of the northern Rocky Mountains is basically a disjunct extension of a coastal ecosystem that was fragmented by the climatic changes created by the uplift of the Cascade Range in the Pliocene. *Crataegus suksdorfii* joins a long list of plant and animal species whose principal distribution is west of the Cascades, but which also occur in the region of maritime climate in the northern Rocky Mountains (Lorain 1988).

The sympatry between *C. suksdorfii* and *C. douglasii* in the northern Rocky Mountains provides us with an opportunity to make more profound judgments of their biological relationships. We now believe that these entities are reproductively isolated by virtue of their ploidal differences likely supplemented by phenological and ecological separation. They can be easily distinguished by a suite of floral and vegetative traits, which in concert with phenological and ecological differences indicate significant genetic divergence. These entities would appear to qualify as segregate species by the criteria of both the biological and taxonomic species concepts.

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ANNOUNCEMENT

NEW MADROÑO EDITOR

The Executive Council of the California Botanical Society is pleased to announce the appointment of Dr. Jon E. Keeley to the position of Editor of Madroño. Dr. Keeley is professor of Biology at Occidental College. His editorship will commence in January 1991 with volume 38. All new manuscripts submitted to Madroño and all returned revisions should be mailed to him at the Department of Biology, Occidental College, Los Angeles, CA 90041. Dr. David J. Keil, who has completed his term as Editor, will be appointed to the Board of Editors to assist with continuity of journal management.